

“Contribution to the History of the Interchange of Pulmonary Gases in the Respiration of Man.” By WILLIAM MARCET, M.D., F.R.S. Received June 9,—Read June 16, 1892.*

I had the honour of communicating a paper to the Royal Society in June, 1891, embodying the results obtained from a first series of inquiries on the interchange of pulmonary gases. The investigation has been continued, and I have had the benefit of the assistance of Mr. G. P. Darnell Smith, B.Sc., in the present work. I am greatly indebted to Mr. Smith for many useful suggestions; while our discussions have been fruitful on many occasions.

The apparatus used for the estimation of carbonic acid and oxygen has been fully described in my former paper, but, as the drawing of the eudiometer employed could not be inserted in that communication, it is appended to this paper together with an explanation of the construction of the instrument.

The key to a method of investigation calculated to give correct information on the interchange of the respiratory gases is to be found in the means adopted for the determination of the volumes of air inspired and expired. C. Speck in his experiments, inspired a measured volume of air from a bell-jar, carefully balanced over a water trough, and expired it into another, the volumes of air inspired and expired being thus determined by direct measurement. Messrs. Hanriod and Richet used gas meters instead of bell-jars. In my former inquiry, after trying how closely experiments with bell-jars agreed with each other, it was found that the results obtained were not sufficiently reliable to be used except in the form of means; on that account, the object was attained by calculation, assuming that the volume of nitrogen in the air expired was exactly the same as the volume of nitrogen in the air inspired; consequently the volume of nitrogen expired was proportional to the volume of air inspired.

It has occurred to me that an objection to this means of determining the volume of air inspired might be raised on the ground that it is unscientific to adopt a method of inquiry based on an assumption, although the investigations of Regnault and Reiset have apparently placed what I call an assumption on the footing of an acknowledged fact. There was consequently a gap to fill up, as it was necessary to ascertain whether nitrogen is either absorbed in the blood or given out, or whether it takes no appreciable part in the respiratory process; with this object, an experiment was made by re-breathing a known volume of air in a bell-jar, and determining afterwards the volume of nitrogen present in this air, but the

* Revised August, 1892.

method proved unsatisfactory. Another experiment was made with three bell-jars—a small one, of a capacity of 10 litres, being placed between two others which held, when full, 40 litres each; the three bell-jars were connected with each other by india-rubber tubing in the course of which an apparatus was disposed for the absorption of carbonic acid. The person under experiment breathed out of and into the middle and smaller bell-jar, which held at the time 5 or 6 litres of air, while a known volume of air was driven from one of the large bell-jars into the other, through the smaller receiver and back again. The carbonic acid absorbed was replaced by oxygen gas. The principle of the method was indeed the same as that adopted by Regnault and Reiset, and more recently by Messrs. Jolyet, Bergonié, and Sigalas.* Great difficulty, however, was met with in this experiment, especially from the tension of gases in the bell-jars, and it was ultimately given up.

At last the simplest method was resorted to; although, the results of the experiments varying somewhat widely from each other, this process necessitated the adoption of means.

The experiments were conducted much on the same principle as those made by C. Speck, every precaution being taken to carry them out as correctly as possible. For this purpose, 40 litres of atmospheric air were introduced into one of my bell-jars, the air being saturated by passing it slowly through a glass vessel holding cotton-wool wetted with tepid water. Air was inspired from this bell-jar through the nose, with nose-pieces fitting closely into the nostrils, and expired from the mouth into another bell-jar, also holding 40 litres; corrections were made for slight differences between the bell-jars and for temperatures. In some of the experiments a valve was placed in the tract of the air inspired, and in others no valve was used, but the inspiratory and expiratory india-rubber tubes were pinched alternately with the fingers to prevent any regurgitation. Notwithstanding every care to breathe as naturally as possible, the relations between the volumes of air inspired and expired were occasionally found to differ widely from each other. On this account it has been found necessary to reject a certain number of these experiments, which yielded figures clearly far distant from those they should have given; and I have finally a series of ten experiments to record, in which it will be observed that, although there is a very marked difference between the figures obtained, still the means show that nitrogen takes no appreciable part in the phenomenon of respiration, if concerned at all in this function.

The following are the results obtained, placed in a tabular form—

* References to these papers were given in my former communication.

No. of experiment.	Volumes of air observed.		Volumes of air inspired, obtained by calculation from the volume of nitrogen found in the air expired.
	Inspired.	Expired.	
1 (self)	33,944 c.c.	33,654 c.c.	34,000 c.c.
2 "	34,238 "	33,833 "	33,972 "
3 "	33,686 "	33,445 "	33,783 "
4 "	33,705 "	33,585 "	33,843 "
5 (Mr. Smith) ...	33,996 "	33,840 "	34,262 "
6 " ...	33,945 "	33,774 "	33,953 "
7 (self)	33,226 "	32,886 "	33,106 "
8 "	34,553 "	34,366 "	34,658 "
9 (Mr. Smith) ...	33,194 "	32,926 "	33,101 "
10 " ...	32,912 "	32,585 "	32,754 "
Means	33,740 "	33,489 "	33,743 "

In this table the first column of figures, on the left, shows the volumes of air inspired, as measured in the bell-jar from which the air was breathed; the second column shows the corresponding volumes of air expired as determined in the second receiver. The third column gives the volumes of air inspired, calculated from the assumption that the whole of the nitrogen exhaled is also inhaled.

It will be observed that the mean of the volumes in the third column is all but exactly the same as the mean of the volumes in the first column, the difference being only by 3 c.c.; hence the obvious conclusion that nitrogen takes no appreciable part, or no part at all in the interchange of the pulmonary gases.

It follows from the harmony found to exist between the mean volumes of air actually inspired and the mean volumes of air inspired determined by calculation, that the corresponding volumes of nitrogen, of oxygen consumed, and oxygen absorbed and retained in the blood, whether found or calculated, will also be practically the same; this is set forth clearly in the next table.

These experiments show most satisfactorily that the method adopted to obtain the volumes of air inspired by *calculation* can be trusted as correct; and, therefore, that not only the means obtained by that method, but also every single experiment, may be accepted as giving a reliable result. A certain amount of training was, however, required before the results could be considered as fit for recording.

The next point for consideration refers to the influence of changes of temperature on the consumption of oxygen per minute, or, in other words, on the carbonic acid produced and oxygen absorbed. These experiments have been made on myself and Mr. Smith while under the influence of food, and an additional number were made on

	Nitrogen actually present in air inspired.	Nitrogen by calculation in air inspired.	Oxygen consumed.		Carbonic acid produced.	Oxygen absorbed per minute.		Duration of the experiment.
			Found.	Calculated.		Found.	Calculated.	
W. M.	26,810 c.c.	26,853 c.c.	1775 c.c.	1806 c.c.	1460 c.c.	48.3 c.c.	53.7 c.c.	6 m. 31 s.
W. M.	27,052 "	26,841	1816 "	1760 "	1622 "	30.7 "	21.9 "	6 " 19
W. M.	26,614 "	26,695	1873 "	1895 "	1557 "	45.0 "	48.2 "	7 " 1
W. M.	26,634 "	26,741	1857 "	1886 "	1628 "	39.1 "	44.1 "	7 " 17
D. S.	26,864 "	27,074	2240 "	2296 "	1874 "	49.6 "	57.1 "	7 " 23
D. S.	26,823 "	26,830	2104 "	2105 "	1926 "	26.4 "	26.6 "	6 " 44
W. M.	26,249 "	26,154	1887 "	1862 "	1642 "	32.1 "	28.8 "	7 " 38
W. M.	27,297 "	27,380	2005 "	2027 "	1735 "	38.8 "	41.9 "	6 " 58
D. S.	26,224 "	26,150	1814 "	1768 "	1598 "	36.4 "	28.8 "	6 " 5
D. S.	26,004 "	25,879	1859 "	1826 "	1657 "	33.4 "	27.9 "	6 " 3
Means	26,657 c.c.	26,660 c.c.	1923 c.c.	1923 c.c.	1669 c.c.	37.98 c.c.	37.90 c.c.	6 " 48

Mr. Smith while fasting; hence, in his case, the experiments show the influence of food on the interchange of pulmonary gases. I regret that in the present inquiry no experiments were made on myself while fasting, and that those, fasting, on Mr. Smith are too few to show any influence of temperature under this condition. It would have been, of course, more satisfactory to eliminate the influence of food while inquiring into the action of differences of temperature on the interchange of the pulmonary gases. The results obtained show the effects of a change of temperature on the chemical phenomena of respiration to vary somewhat with different persons, some being more disposed than others to react against an accession of cold by an increased production of carbonic acid. In my case, the effect is very obvious, as seen in the following table (p. 218).

First of all, if the means of the oxygen consumed per minute, the carbonic acid produced, and the oxygen absorbed, also per minute, be compared with the corresponding figures obtained under the influence of food in my former inquiry,* they will be found to harmonise with them in a marked degree; they are as follows:—

	In former paper.	Obtained recently.
Oxygen consumed.....	248 c.c.	247 c.c.
Carbonic acid produced...	218 „	212 „
Oxygen absorbed.....	30·2 „	35·7 „

The oxygen consumed is nearly exactly the same in both cases, varying by only 1 c.c. The carbonic acid produced is a little lower in the recent experiments, and the oxygen absorbed somewhat higher.

The slight difference between the carbonic acid produced in each set of experiments, and also the difference, which is rather greater, between the figures found for oxygen absorbed in the two series of experiments, 30·2 and 35·7, are probably owing to the precaution taken in the recent inquiry of allowing half an hour's perfect rest, in the recumbent posture, before commencing the experiment. Formerly the time of rest had been limited to from five minutes to a quarter of an hour, when the pulse and breathing had become perfectly regular; but it was subsequently found that half an hour at least should be allowed before collecting the air expired for analysis, in order to ensure the body being in a perfect state of rest.

The table has been disposed in a graphic form, the curves showing, at a glance, the influence of temperature on the interchange of pulmonary gases in my case; this influence† may be summarised as follows:—

* 'Roy. Soc. Proc.,' June, 1891, vol. 50.

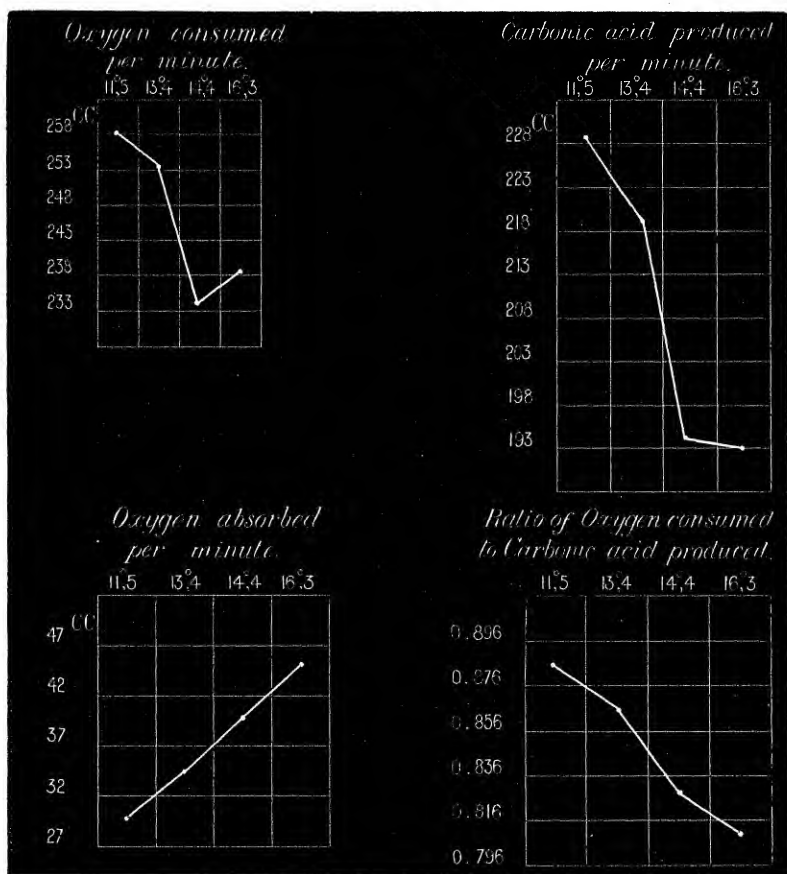
† The influence of cold or heat in the present experiments applies exclusively to

Table showing the Influence of Temperature on the Carbonic Acid Produced and Oxygen Absorbed per minute. (W. Marcet, aged 64, under experiment.)

Duration of experiment.	Time after full meal.	Temperature of laboratory.	Oxygen consumed.	Carbonic acid produced.	Oxygen absorbed.	Ratio of O. consumed to CO ₂ produced.	Ratios grouped two by two.
m. s. 7 8	h. m. 2 15	° C. 11·4	c.c. 262	c.c. 238	c.c. 24·9	0·909	0·916
7 0	2 35	11·4	259	239	20·4	0·923	
8 11	1 45	11·7	257	211	46·1	0·821	0·821
7 57	2 15	13·4	243	211	31·8	0·868	0·868
7 22	1 30	13·5	265	228	37·3	0·860	0·860
7 55	2 45	14·4	229	194	35·6	0·844	0·826
8 36	2 55	14·4	240	194	46·0	0·808	
7 50	2 55	14·4	238	201	37·1	0·844	0·831
8 6	3 10	14·4	232	190	42·2	0·819	
8 20	2 55	16·3	239	193	45·9	0·808	0·808
Means 7 51	2 30	13·5	246	210	36·7	0·850	

The experiments bracketed have been made at the same sitting.

- 1st. The oxygen consumed falls as the temperatures rise.
- 2nd. The carbonic acid produced falls at a similar rate, under the same conditions of temperature, or as the temperatures rise.
- 3rd. The oxygen absorbed increases as the temperatures rise.
- 4th. The ratio of oxygen consumed to carbonic acid produced falls as the temperatures increase. This is a natural consequence of the corresponding variation of the oxygen consumed and carbonic acid produced.



This chart is made by grouping the temperatures as follows, and classing the figures for oxygen consumed, carbonic acid produced, winter temperatures, when an accession of cold is to be met by an increased oxidation in the body. Summer temperatures may act altogether in a different way.

oxygen absorbed, and ratios (under the form of means), together with their respective temperatures:—

	11°·4	13°·4	14°·4	16°·3
	11°·4	13°·5	14°·4	
	11°·7		14°·4	
			14°·4	
Means	11°·5	13°·4	14°·4	16°·3

Of course it cannot be expected, in a work of this kind, that tracings will be perfectly regular; hence in the tracing for oxygen consumed we observe a slight abnormal rise between 14°·4 and 16°·3. This is probably owing to the weather being cold outside; the experiment was done on the 24th of February; the maximum temperature of that day in the open air was 9° C. (Wimbledon Park), and the body was partly under this cooling influence, although the temperature of the laboratory, at University College, heated with hot-water pipes, was 16°·3. The tracing for carbonic acid produced also exhibits irregularities, but the curves show distinctly that, at all events in my case, changes of temperature exert a very positive influence on the interchange of the pulmonary gases.

If the temperatures of the atmosphere in which the experiments are made be divided into two groups, one group including the lowest and another the highest, and a table constructed, into which the carbonic acid produced and oxygen absorbed are entered together with their corresponding temperatures, this table will be as follows:—

Low temperature.			High temperature.		
Temperature.	CO ₂ produced. per min.	O absorbed per min.	Temperature.	CO ₂ produced per min.	O absorbed per min.
° C.	c.c.	c.c.	° C.	c.c.	c.c.
11°·4	238	24·9	14°·4	194	35·6
11°·4	239	20·4	14°·4	194	46·0
11°·7	211	46·1	14°·4	201	37·1
13°·4	211	31·8	14°·4	190	42·2
13°·5	228	37·3	16°·3	193	45·9
Means 12°·3	225	32·1	14°·8	194	41·4
Mean ratio of CO ₂ produced to O absorbed = 0·143.			Mean ratio of CO ₂ produced to O absorbed = 0·213.		

The mean ratio of CO_2 produced to O absorbed is, therefore, very different according to temperatures; it is much lower in relatively cold than in warmer temperatures; hence the interesting fact that the absorption into the blood of that proportion of oxygen consumed which is not transformed into carbonic acid is not concerned in the production of heat towards resisting external cold. This is clearly the case, as the colder the atmosphere the less the proportion of oxygen consumed as *absorbed* in opposition to the proportion consumed towards the production of carbonic acid, which is markedly increased. A similar effect of temperature is met with in the experiments reported in my former paper. Out of six experiments made on myself under the influence of food, two were carried out 2 hrs. 25 mins. and 1 hr. and 40 mins. respectively after a meal, when the laboratory in winter was much below its usual temperature, the readings being $10^{\circ}4$ C. and 12° C.; on these occasions the oxygen absorbed per minute was 27 c.c. and 24.8 c.c. respectively, and the mean ratio between the CO_2 produced and O absorbed was $\frac{25.9}{228} = 0.114$; while when the laboratory was comfortably warm, at a mean temperature of $16^{\circ}8$ C., the mean volume of oxygen absorbed was 32.4 c.c., and the ratio $\frac{32.4}{213} = 0.152$. Hence, again, the ratios were lower in low than in high temperatures, which means that in my case in low temperatures less oxygen is absorbed, relatively to the carbonic acid produced, than in high temperatures. The experiments *while fasting* reported in my former paper were all made when the laboratory was comfortably warm, and cannot be utilised towards showing the influence of temperature.

With Mr. Darnell Smith, who kindly submitted to experiment, the results are as follows:—

Table showing the Influence of Temperature and of the Ingestion of Food on the CO₂ produced and O absorbed per minute. (Darnell Smith, aged 23, under experiment.)

	Duration of experiment.		Time after a full meal.		Temperature of the air.	O consumed.	CO ₂ produced.	O absorbed.	Ratio of O consumed to CO ₂ produced.
Under the Influence of Food.									
Means of two experiments ..	m.	s.	h.	m.	c.c.	c.c.	c.c.	c.c.	
"	8	5	2	55	13.1	275	222	51.9	0.811
"	8	5	2	20	13.2	289	229 } 238	60.6	0.792
"	8	6	2	35	13.9	289	240 } 238	40.3	0.863
"	8	4	2	25	13.9	283	233 } 231	50.0	0.824
"	7	33	2	55	15.0	288	229 } 231	59.0	0.795
"	8	34	2	35	16.7	263	221 } 222	41.5	0.842
"	7	44	2	33	22.2	270	223 } 222	46.9	0.826
Means	8	11	2	30	15.4	280	229	50.0	0.822
Fasting.									
Means of two experiments ..	8	30	5	15	12.9	246	211	35.8	0.855
"	8	32	5	15	15.8	257	225	32.2	0.875
"	8	59	5	40	17.2	246	212	34.2	0.861
Means	8	40	5	23	15.3	250	216	34.1	0.864

In Mr. Smith's case there are actually seven pairs of experiments (fourteen altogether) made under the influence of food. Each experiment was repeated at the time, and the means of the pairs were taken and recorded.

Grouping these pairs of experiments two-by-two, as shown in this last table, the volumes of oxygen consumed will be found to exhibit a slight decrease as the temperatures rise, the carbonic acid produced also shows a slight tendency to fall with the increase of temperature. The oxygen absorbed, which in my case is unmistakably increased with a rise in temperature, is not found to undergo a similar change, but remains nearly the same throughout; there being a slight fall at the two highest temperatures.

With reference to the influence of food on the interchange of the pulmonary gases, the experiments made on Mr. Smith fasting, or when a desire for food was felt about five hours after breakfast, showed a considerable falling off in the oxygen consumed, carbonic acid produced, and oxygen absorbed. Corresponding experiments have been reported in my former paper. Mr. Russell, who assisted me at the time, a young gentleman twenty-one years of age, also exhibited a decrease, though but slight, of oxygen absorbed while fasting, the figures being 33·3 c.c. while fasting, and 37·5 at a mean period of 2 hrs. 16 min. after a full meal. In my case the figures were 35·3 c.c. while fasting and 30·2 under food, which show a slight influence in the opposite direction. It appears, therefore, that the influence of food upon the absorption of oxygen varies with different persons, but that in young and strong people the absorption of oxygen has a decided tendency to increase after a meal.

The results obtained from the present inquiry may be summarised as follows:—

1. Nitrogen acts a part inappreciable, if concerned at all, in the interchange of pulmonary gases.

2. The influence of changes of the atmospheric temperature on the oxygen consumed, carbonic acid produced, and oxygen absorbed, although in the present experiments this influence is more or less interfered with by the phenomena of digestion, is distinct in my case; the oxygen consumed and carbonic acid produced increasing with falling temperatures, while the oxygen absorbed is lessened; and a similar result is obtained from the consideration of the figures given in my former communication. This fact is interesting, perhaps, mainly as showing that the oxygen absorbed is not concerned in the formation of heat in the body towards resisting cold—a function which appears to be limited entirely to the oxidation of carbon into carbonic acid. If, as usually admitted, the blood is limited in its power of taking up oxygen, although this power may apparently vary according to temperatures, then it is obvious that an increased formation of carbonic acid

must necessarily be attended with a falling off in the oxygen absorbed. Cold would thus rob the body of a portion of its oxygen and interfere with those functions of nutrition with which the absorbed oxygen is concerned. This would explain the hibernation of animals—their functions are arrested because the whole of the oxygen they consume in winter is used up towards the formation of carbonic acid, and there is none left to carry on the phenomena of nutrition. It would also account for the sleepiness or stupor well known to be produced by intense cold.

When Mr. Smith was under experiment the influence of temperature on the oxygen consumed and carbonic acid produced was in the same direction, though much less marked than in my case. The oxygen absorbed does not, however, show the same tendency to decrease with a falling temperature. This does not, I consider, invalidate the result as obtained on myself, the temperature of the air being higher when the experiments were made on Mr. Smith than when they were undertaken on myself, and the body being under the influence of an early spring season in March; while the experiments on myself were made in winter, when the laboratory at times was very cold.

3. The influence of food on the interchange of respiratory gases, although being attended with a rise in the oxygen consumed and carbonic acid expired, apparently varies with reference to the oxygen absorbed. Young and strong persons, requiring a full allowance of food, appear to absorb more oxygen while under the influence of a meal than while fasting, but late in life the oxygen absorbed appears to show little or no tendency to increase after a meal. According to Hanriot and Richet, the carbonic acid produced increases considerably under the influence of food, while the increased absorption of oxygen is but slight.*

In conclusion, I wish to allude shortly to a result embodied in my former communication, and relating to the respiration of air containing an increased proportion of carbonic acid. Five experiments had been made—three on myself and two on my assistant, Mr. Russell. The proportions of CO_2 in the air inspired were respectively 2.13, 3.14, 4.06, 3.79, and 3.91 per cent. It was found that the amount of carbonic acid produced in a given time was lower than when pure air was breathed, and that the oxygen absorbed was greatly increased.

The following table gives the figures obtained for the oxygen absorbed:—

* 'Ann. de Chimie et de Physique,' April, 1891.

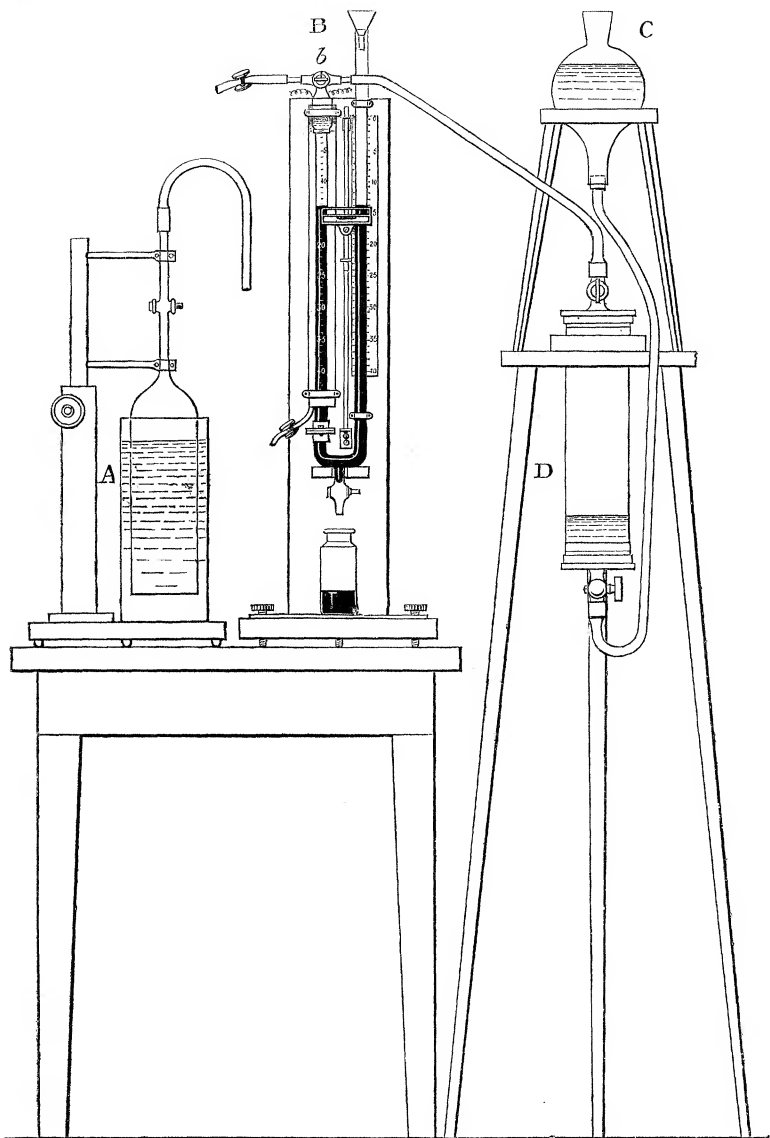
	Per cent. CO ₂ in air inspired.	Oxygen absorbed per minute.	Oxygen absorbed under normal conditions per minute.	Oxygen absorbed retained in the blood as CO ₂ per minute.
Self { 1	2.53	71 c.c.	27	44 c.c.
2	3.54	112 "	27	85 "
3	4.06	127 "	25	102 "
Mr. Russell { 1.	3.79	141 "	25	116 "
2.	3.91	170 "	37	133 "

It will be seen that the oxygen absorbed per minute when carbonic acid was breathed greatly exceeded the oxygen absorbed when pure air was inspired. The figures given in the table for O absorbed under normal conditions, are taken, with one exception, from experiments made at the same sitting as those in which CO₂ was breathed, and therefore compare with them. The excessive volume of oxygen absorbed when air mixed with CO₂ was inhaled must have been owing to the fact that a portion of the oxygen consumed, which under usual circumstances would have been given out as carbonic acid, remained in the blood, obviously as carbonic acid, because of the impeded diffusion in the lungs on account of the CO₂ contained in the air breathed. The actual amount of carbonic acid being thus retained in the blood can be calculated, with what I think a near degree of approximation, by subtracting the oxygen which would have been absorbed in the respiration of pure air from the oxygen actually found to have been absorbed under the influence of the CO₂ inspired.

These figures, varying from 44 c.c. to 133 c.c., are entered in the last column of the table, and show how large a volume of CO₂ may be retained in the blood when air contaminated with CO₂ is used for respiration. This carbonic acid goes on accumulating in the body interfering with the normal phenomena of oxidation. It is very difficult to consider this effect otherwise than poisonous; although under circumstances which admit of the introduction of CO₂ in the blood through another channel than respiration, the gas appears innocuous. Cl. Bernard has shown this to be the case by the injection of CO₂ into the circulation of animals, when the gas found its way out of the body through the lungs without producing any morbid action.

Description of a New Form of Eudiometer.

- A. Receiver containing hydrogen gas.
- B. Eudiometer.
 - b. Three-way stopcock.
- C. Flask holding water.
- D. Cylinder containing the gas for analysis.



The endiometer has the form of a U-tube, drawn into an open neck at its bend, where the opening is controlled with a stopcock. One of the limbs of the instrument, which is graduated, is surrounded by a water jacket, and has an iron cap cemented to it, in which there is a

three-way iron stopcock. A scale is fixed at the back of the open limb, the divisions corresponding exactly to those engraved on the other limb.

The flask C, open at both ends, is full of water, and communicates by india-rubber tubing with the cylinder D, which contains the air for analysis.

The process of analysis is as follows :—The eudiometer is entirely filled with mercury. Next, the hydrogen being placed under a pressure of 1 or 2 inches of water by depressing the receiver, the gas is driven through the three-way cock, while at the same time it is aspirated by a compressed india-rubber syringe, which is suddenly released; this washes out all the atmospheric air from the tube connecting the supply of hydrogen with the eudiometer. The three-way cock being turned so as to connect the hydrogen-receiver with the eudiometer, mercury is let out at the bend of the instrument, when hydrogen is drawn into it, and the volume of the gas recorded. Air from the flask D is admitted into the eudiometer through the india-rubber tube, pressure being exerted by the water held in the flask D, while aspiration is produced by letting out mercury from the eudiometer. The gases are brought under atmospheric pressure by adding or taking out mercury.

The gases are mixed in the eudiometer by means of an india-rubber syringe fitting to the open end of the instrument, where the funnel is shown in the drawing; the syringe is compressed and released repeatedly, thus driving the mercury up and down. The little movable spirit level is convenient, though not indispensable, towards the adjusting of the mercury in the two limbs. I find that such an instrument has been proposed, or used, for similar purposes by G. Lunge ('Chem. Soc. Jl.,' 1892), but the readings are not so reliable as those obtained from two identical scales, one for each limb of the U-tube.

The gases are finally exploded in the usual way.

The process is described in full in my paper read June, 1891, to the Royal Society.

Crappie consumed
per minute
10 15 20 25



Crappie consumed
per minute
10 15 20 25



Crappie consumed
per minute
10 15 20 25



Crappie consumed
per minute
10 15 20 25

